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Short Note

# Upper thermal limits and warming safety margins of coastal marine species – Indicator baseline for future reference

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ABSTRACT

The threat of global warming has driven recent efforts of estimating upper thermal limits of ectothermic species all over the world. The investigation of thermal limits is crucial for the understanding of climate change ecology, since it provides insight into how climate will shape future species distributions. This work estimated the Critical Thermal Maxima (CTMax) of 42 coastal species (Gastropoda, Crustacea, Teleostei, Echinodermata and Cnidaria) in a tropical and a temperate area. The thermal safety margin (CTMax-Maximum Habitat Temperature) and future thermal safety margin (CTMax-(Maximum Habitat Temperature + 3 °C)) of each species was estimated for two alternative habitats, shallow coastal waters and tide pools. The CTMax of tropical species was higher than that of temperate species and no difference was found among the taxonomic groups tested. Thermal safety margins were larger for temperate species, than for tropical species, and considerably larger for shallow waters than for tide pools. Most tropical species had negative safety margins in tide pools (with only two exceptions), while most temperate species had positive safety margins (with only three exceptions). Future thermal safety margins for tide pools were negative for all tropical organisms and also for most of their temperate counterparts. This work adds to the data collection already available for the study areas, raising the number of species with known upper thermal limits to 100. These estimations do not take into account phenotypical acclimation, nor genetic adaptation, to future temperatures, which are likely to occur. However, they constitute important values for future reference, allowing insights into the adaptation capacity of coastal species, as well as basis to explain future distribution shifts and/or local extinctions.

## 1. Introduction

Understanding the thermal limits of organisms has long been a subject of interest among biologists (Angilletta, 2009). Such interest has increased in the latest decades due to pressing concerns related to anthropogenic climate warming. To predict the likely consequences of warming requires detailed knowledge on how close species are to their thermal limits.

The vulnerability of each species to warming will ultimately depend on its thermal limits, acclimation response and genetic adaptation potential (e.g. Stillman, 2003; Somero, 2010), which remain unknown for most species. This way experimental estimation of species' thermal limits is a welcome addition to the body of knowledge concerning climate warming.

Another important aspect is the present and future thermal conditions of the species' habitat. Numerous studies have shown that tropical habitats attain temperatures that are closer to the upper thermal limit of its inhabiting species, than temperate habitats (e.g. Deutsch et al., 2008, Vinagre et al., 2016, 2018). This way, although the tropics are expected to warm at a slower rate than temperate latitudes, tropical organisms should be more vulnerable to warming than their temperate counterparts.

It is also important to consider that many species, particularly marine coastal ectotherms, occupy different habitats throughout their life-cycles and are thus exposed to different thermal regimes (Madeira et al., 2012a, 2014, Vinagre et al., 2012, 2018). During the larval and juvenile stage many coastal organisms occur in shallower waters, that attain higher temperatures than offshore coastal waters. Some of them even remain in tide pools during the ebb tide (Dias et al., 2016). These small bodies of water can reach temperatures that are above the

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thermal limits of many species, with lethal effects already observed in tropical coasts (Hiatt and Strasburg, 1960; Andrades et al., 2016).

Vinagre et al. (2018) tested the upper thermal limits and acclimation capacity of 46 coastal species that occur in tide pools and concluded that tropical tide pools can act as ecological traps for coastal species during heat waves and should be even more deleterious in the future due to climate warming.

The present study reports on the upper thermal limits (Critical Thermal Maxima, CTMax) of 42 additional coastal species, both tropical and temperate, that occur in shallow coastal waters and tide pools, and that could not be included in Vinagre et al. (2018) because their acclimation was not tested. The thermal safety margin (TSM = CTMax – Maximum Habitat Temperature) of each species was estimated for two alternative habitats, shallow coastal waters and tide pools. The future thermal safety margin was also estimated (CTMax-(Maximum Habitat Temperature + 3 °C)).

The CTMax and TSM values provided here will be useful references for future studies on the thermal ecology and adaptation capacity of coastal species, as well as a possible basis to explain future distribution shifts and/or local extinctions.

## 2. Material and methods

Coastal organisms were collected in tide pools, by hand or using hand-nets, in a tropical and a temperate coastal area, in Brazil (São Sebastião – Ubatuba, São Paulo State) and Portugal (Cabo Raso – Avencas), respectively, in the summer of 2015. Two sites in each area were chosen for the collection of organisms (23°49′S; 45°25′W and 23°27′S; 45°03′W in Brazil and 38°41′ N; 9°21′ W and 38°26′N; 8°50′W in Portugal). Seven pools were selected in each area, all of them located in the lower intertidal, with a mean depth of 0.3 m and a maximum depth of 0.5 m.

### 2.1. Experimental setup

Organisms were kept in closed-system aquaria with aerated seawater and salinity at 35‰. Different species were separated into different aquaria. Organisms were fed daily *ad libitum* and starved for 24 h prior to temperature trials. Carnivorous Gastropoda, Crustacea, Teleostei, Echinodermata and Cnidaria were fed with frozen shrimp muscle and commercial fish pellets. Herbivorous and omnivorous gastropods were provided natural rocks covered with the macroalgae *Ulva* sp. and commercial fish pellets.

Tropical organisms were kept for seven days at 29.0 °C ( ± 0.5 °C) and temperate organisms at 22.0 °C ( ± 0.5 °C), the same temperature as found in the natural environment at the time of capture, for minimal thermal disturbance. After this acclimation period, the critical thermal maximum (CTMax) was determined, following the same protocol as Vinagre et al. (2018).

The CTMax method is a well-established dynamic method of quantifying the upper thermal limits (e.g. Lutterschmidt and Hutchison, 1997; Mora and Ospina, 2001). It is defined as the “arithmetic mean of the collective thermal points at which the end-point is reached”, the end-point being loss of balance. The criteria for the determination of the end-point was the same followed by (Mora and Ospina, 2001; Madeira et al., 2012b; Vinagre et al., 2015, 2018).

The rate of water temperature increase was 1 °C/15 min both for tropical and temperate organisms, as a standardized way to evaluate aquatic organisms and thus obtain comparable results (Bennett et al., 2018). A digital thermometer was used to register the end-point. The total length of all individuals was measured at the end of the CTMax experiment (Table 1).

Thermal safety margins (TSM = CTMax-Maximum habitat temperature) were estimated for all species for two different habitats where they occur, shallow coastal waters (TSMcoast) and tide pool waters (TSMpool). The mean maximum habitat temperature for coastal waters was 28.4 °C for the tropical site and 22.2 °C for the temperate site, based on satellite data from www.seatemperature.org. The maximum habitat temperature for tide pools was 41.5 °C for the tropical site and 30.6 °C for the temperate site, based on Hobo temperature probes attached to the bottom of random tide pools in 2014–2016 (for more details see Vinagre et al., 2018). Future safety margins, for the year 2100 (TSMcoast2100 and TSMpool2100), were defined as the difference between the CTMax of each species and the maximum habitat temperature plus 3 °C, based on IPCC projections for 2100 (IPCC, 2013).

**Table 1**
Taxonomic group and mean length of the individuals used in the experiments.

| | Species | Lt (mm) | SD (mm) |
|---|---|---|---|
| Tropical | | | |
| Gastropoda | *Costoanachis sertulariarum* | 7.94 | 1.06 |
| Gastropoda | *Hastula cinerea* | 33.93 | 6.31 |
| Gastropoda | *Leucozonia nassa* | 33.77 | 5.79 |
| Gastropoda | *Pisania auritula* | 17.61 | 5.04 |
| Gastropoda | *Astraea olfersii* | 37.60 | 3.10 |
| Gastropoda | *Cerithium atratum* | 30.23 | 2.23 |
| Gastropoda | *Astraea phoebia* | 23.21 | 8.30 |
| Gastropoda | *Ischnochiton striolatus* | 7.47 | 1.17 |
| Crustacea | *Pilumnus reticulatus* | 8.71 | 2.14 |
| Crustacea | *Acanthonyx* sp. | 12.00 | 0.00 |
| Crustacea | *Charybdis hellerii* | 33.45 | 12.10 |
| Crustacea | *Petrolisthes armatus* | 9.33 | 1.22 |
| Crustacea | *Mithraculus forceps* | 6.09 | 0.83 |
| Crustacea | *Acantholobulus schmitti* | 8.96 | 2.10 |
| Crustacea | *Hippolyte obliquimanus* | 15.40 | 1.48 |
| Crustacea | *Lysmata lipkei* | 35.20 | 7.41 |
| Crustacea | *Calcinus tibicen* | 40.00 | 7.04 |
| Crustacea | *Paguristes tortugae* | 33.60 | 10.74 |
| Crustacea | *Arenaeus cribrarius* | 34.67 | 2.89 |
| Teleostei | *Parablennius marmoreus* | 39.87 | 6.08 |
| Teleostei | *Malacoctenus delalandii* | 39.17 | 10.68 |
| Teleostei | *Diapterus rhombeus* | 32.50 | 1.41 |
| Teleostei | *Sphoeroides testudineus* | 56.00 | 4.95 |
| Temperate | | | |
| Gastropoda | *Littorina saxatilis* | 16.75 | 9.05 |
| Gastropoda | *Patella depressa* | 27.58 | 7.66 |
| Gastropoda | *Chaetopleura angulata* | 46.00 | 4.85 |
| Gastropoda | *Leptochiton algesirensis* | 10.50 | 4.23 |
| Gastropoda | *Patella vulgata* | 24.29 | 6.81 |
| Gastropoda | *Siphonaria pectinata* | 16.40 | 2.53 |
| Crustacea | *Pachygrapsus marmoratus* | 17.72 | 5.93 |
| Crustacea | *Carcinus maenas* | 33.33 | 5.57 |
| Crustacea | *Porcellana platycheles* | 8.00 | 1.41 |
| Crustacea | *Pirimela denticulata* | 15.20 | 1.64 |
| Crustacea | *Anapagurus laevis* | 18.80 | 3.90 |
| Crustacea | *Necora puber* | 19.40 | 1.95 |
| Teleostei | *Atherina* sp. | 33.50 | 2.66 |
| Teleostei | *Diplodus cervinus* | 44.25 | 17.48 |
| Teleostei | *Liphophrys trigloides* | 50.00 | 21.28 |
| Echinodermata | *Marthasteria glacialis* | 49.30 | 5.02 |
| Echinodermata | *Asterina gibbosa* | 28.00 | 8.96 |
| Echinodermata | *Ophiura ophiura* | 8.00 | 2.24 |
| Cnidaria | *Actinia equina* | 5.33 | 0.60 |

### 2.2. Data analysis

Factorial analyses of variance (ANOVA) were conducted to test the effect of region (tropical *vs* temperate) and taxonomic group in CTMax, TSMcoast, TSMpool, TSMcoast2100 and TSMpool2100, using average values for each species as replicates. A one-way ANOVA was conducted to test for differences among the different TSMs (TSMcoast, TSMpool, TSMcoast2100 and TSMpool2100) for each taxonomic group, in each region, using average values for each species as replicates, followed by Tukey post-hoc tests. Prior to these tests, normality and homoscedasticity were confirmed.

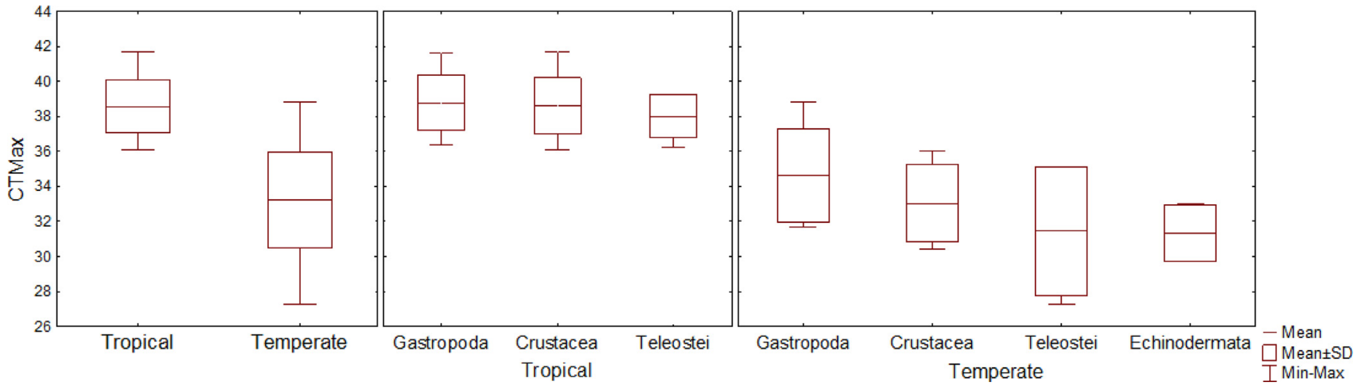


**Fig. 1.** Distribution of the values of CTMax of tropical and temperate organisms.

## 3. Results

CTMax of tropical species was higher than that of temperate species and no difference was found among the taxonomic groups tested (region: $F = 55.51$, $p < 0.01$; group: $F = 2.18$, $p = 0.13$; region * group: $F = 0.91$, $p = 0.41$) (Fig. 1). The highest CTMax recorded was that of the speckled swimming crab *Arenaeus cribrarius* at 41.70 °C, in the tropical area (Table 2). The lowest CTMax among tropical species was that of the shrimp *Hippolyte obliquimanus* at 36.09 °C (Table 2). These species also presented the highest and lowest thermal safety margins among tropical species, respectively (Table 2). The highest CTMax among temperate species was that of the limpet *Patella vulgata* at 38.85 °C, while the lowest was that of *Atherina* sp at 27.27 °C (Table 2). These species also presented the highest and lowest thermal safety margins among temperate species, respectively (Table 2).

TSM for coastal waters presented no difference among regions, nor among taxonomic groups, both in the present (region: $F = 1.14$, $p = 0.29$; group: $F = 2.18$, $p = 0.13$; region * group: $F = 2.18$, $p = 0.13$) and in the future (region: $F = 1.14$, $p = 0.29$; group: $F = 2.18$, $p = 0.13$; region * group: $F = 2.18$, $p = 0.13$). TSM for tide pools presented differences among regions, being higher in the temperate area, but not among taxonomic groups, both in the present (region: $F = 56.62$, $p < 0.01$; group: $F = 2.18$, $p = 0.13$; region * group: $F = 0.91$, $p = 0.41$) and in the future (region: $F = 37.83$, $p < 0.01$; group: $F = 2.18$, $p = 0.13$; region * group: $F = 0.91$, $p = 0.41$). Both tropical and temperate species presented positive present-day thermal safety margins in shallow coastal waters, ranging from 7.69 to 13.30 °C for tropical organisms, and from 5.07 to 16.65 °C for temperate organisms (Fig. 2, Table 2). Future safety margins in coastal waters were also positive for all species both in the tropics and in the temperate area, ranging from 4.69 to 10.30 °C, and from 2.07 to 13.65 °C, respectively (Fig. 2, Table 2).

Most tropical species had negative safety margins in tide pools, ranging from to −5.41 to 0.20 °C (Fig. 2, Table 2). Only two tropical species had positive safety margins in tide pools, the sea snail *Costoanachis sertulariarum* and the crab *Arenaeus cribrarius* (Table 2). Most temperate species had positive safety margins, with only three exceptions, the hermit crab *Anapagurus laevis*, the sand smelt *Atherina* sp, and the seastar *Ophiura ophiura*. Future safety margins for tide pools were negative for all tropical organisms, ranging from −2.80 to −8.41 °C, and also for most of their temperate counterparts, ranging from −7.33 to 4.25 °C (Fig. 2, Table 2).

Comparison of TSMs (TSMcoast, TSMpool, TSMcoast2100 and TSMpool2100) for each taxonomic group, and for each region, revealed consistent differences between TSM for coastal water and for tide pools (both in the present and in the future), for all taxonomic groups (except Cnidaria, which was not tested since it contained only one species) (Fig. 2). TSM for coastal waters was always significantly higher than for tide pools, for all groups, in the present and in the future, both in the tropics (Gastropoda: $F = 189.99$, $p < 0.01$; Crustacea: $F = 260.70$, $p < 0.01$; Teleostei: $F = 153.41$, $p < 0.01$) and in the temperate zone (Gastropoda: $F = 29.99$, $p < 0.01$; Crustacea: $F = 37.76$, $p < 0.01$; Teleostei: $F = 6.80$, $p = 0.01$; Echinodermata: $F = 34.75$, $p < 0.01$) (Fig. 2).

## 4. Discussion

This study adds to the current body of knowledge that clearly shows that tropical species are living closer to their upper thermal limits than temperate species and that this phenomenon is irrespective of animal group. The decline in thermal safety margins with decreasing latitude, from temperate to tropical regions, has been shown to be common for a wide range of ectotherms, including insects, lizards, turtles and frogs (e.g. Deutsch et al., 2008; Duarte et al., 2012), as well as crabs, fish and molluscs (e.g. Helmuth et al., 2006; Noyola et al., 2013a,b; Paschke et al., 2013; Zúñiga et al., 2013; Morley et al., 2014; Salas et al., 2014; Díaz et al., 2015; Cumillaf et al., 2016; Vinagre et al., 2016, 2018; Rodríguez-Fuentes et al., 2017).

The present work also adds 42 species to the 46 species already characterized in terms of CTMax, TSM and acclimation capacity by Vinagre et al. (2018), for the same tropical and temperate sites, most probably making these shallow coastal ecosystems the best studied ecosystems in the world in what concerns individual species thermal limits, with a total of 88 studied species. If we add to this number, the 12 additional species tested (albeit with a different thermal ramp) for the same sites by Madeira et al. (2012b) and Vinagre et al. (2016) we reach a total of 100 species (Fig. 3). This means that the most common shallow water species were characterized in these two ecosystems.

This information will be very useful for the understanding of climate warming ecology in the future, as these estimates will be valuable reference values for many potential studies. Given that highly defined complex food webs in these two ecosystems have also been characterized (Mendonça et al., 2018), it is now possible to investigate the role of thermally vulnerable species in the food web network. They can also be sequentially removed according to their thermal vulnerability and the networks reassessed in terms of structure, secondary extinctions and species persistence.

Additionally, these reference values will be valuable for future comparison, particularly in the year 2100, since the warming estimates used here and, in most studies, refer to that year. Will TSM estimates, based on CTMax and maximum habitat temperatures, be a good predictor of local population decline or extinction? Will tide-pools in these areas suffer a massive decrease in the number of species that inhabit them? Given that an increase in 3 °C may be conservative, will we see these changes before 2100? Continued studies in these areas will provide answers to these questions. These values will also be important to understand distribution changes of these species over larger areas.

Phenotypical acclimation, genetic and epigenetic adaptation will

**Table 2**
Taxonomic group, sample size (N), CTMax and thermal safety margins in coastal waters and in tide pools in the present (CTMax-Maximum habitat temperature) and in the future (CTMax-(Maximum habitat temperature + 3 °C)). SD stands for standard deviation. Negative thermal safety margins are presented in red.

| | Species | N | CTMax (°C) | SD | Thermal Safety Margin (°C) | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Coastal waters | Tide pools | Coastal waters | Tide pools |
| | | | | | Present | Present | Future | Future |
| Tropical | | | | | | | | |
| Gastropoda | *Costoanachis sertulariarum* | 21 | 41.64 | 0.51 | 13.24 | 0.14 | 10.24 | −2.86 |
| Gastropoda | *Hastula cinerea* | 30 | 39.57 | 0.67 | 11.17 | −1.93 | 8.17 | −4.93 |
| Gastropoda | *Leucozonia nassa* | 8 | 39.01 | 0.56 | 10.61 | −2.49 | 7.61 | −5.49 |
| Gastropoda | *Pisania auritula* | 5 | 38.86 | 1.01 | 10.46 | −2.64 | 7.46 | −5.64 |
| Gastropoda | *Astraea olfersii* | 9 | 36.38 | 0.61 | 7.98 | −5.12 | 4.98 | −8.12 |
| Gastropoda | *Cerithium atratum* | 14 | 37.06 | 0.99 | 8.66 | −4.44 | 5.66 | −7.44 |
| Gastropoda | *Astraea phoebia* | 4 | 38.53 | 1.15 | 10.13 | −2.97 | 7.13 | −5.97 |
| Gastropoda | *Ischnochiton striolatus* | 4 | 39.10 | 0.00 | 10.70 | −2.40 | 7.70 | −5.40 |
| Crustacea | *Pilumnus reticulatus* | 7 | 37.86 | 0.63 | 9.46 | −3.64 | 6.46 | −6.64 |
| Crustacea | *Acanthonyx* sp. | 2 | 37.55 | 0.00 | 9.15 | −3.95 | 6.15 | −6.95 |
| Crustacea | *Charybdis hellerii* | 11 | 38.26 | 0.99 | 9.86 | −3.24 | 6.86 | −6.24 |
| Crustacea | *Petrolisthes armatus* | 9 | 39.19 | 0.56 | 10.79 | −2.31 | 7.79 | −5.31 |
| Crustacea | *Mithraculus forceps* | 11 | 38.53 | 0.47 | 10.13 | −2.97 | 7.13 | −5.97 |
| Crustacea | *Acantholobulus schmitti* | 23 | 37.79 | 0.65 | 9.39 | −3.71 | 6.39 | −6.71 |
| Crustacea | *Hippolyte obliquimanus* | 26 | 36.09 | 0.47 | 7.69 | −5.41 | 4.69 | −8.41 |
| Crustacea | *Lysmata lipkei* | 10 | 37.28 | 0.15 | 8.88 | −4.22 | 5.88 | −7.22 |
| Crustacea | *Calcinus tibicen* | 5 | 40.32 | 1.13 | 11.92 | −1.18 | 8.92 | −4.18 |
| Crustacea | *Paguristes tortugae* | 5 | 40.02 | 1.26 | 11.62 | −1.48 | 8.62 | −4.48 |
| Crustacea | *Arenaeus cribrarius* | 3 | 41.70 | 0.00 | 13.30 | 0.20 | 10.30 | −2.80 |
| Teleostei | *Parablennius marmoreus* | 15 | 36.73 | 1.15 | 8.33 | −4.77 | 5.33 | −7.77 |
| Teleostei | *Malacoctenus delalandii* | 6 | 36.20 | 0.33 | 7.80 | −5.30 | 4.80 | −8.30 |
| Teleostei | *Diapterus rhombeus* | 2 | 38.90 | 0.14 | 10.50 | −2.60 | 7.50 | −5.60 |
| Teleostei | *Sphoeroides testudineus* | 2 | 38.80 | 0.00 | 10.40 | −2.70 | 7.40 | −5.70 |
| Temperate | | | | | | | | |
| Gastropoda | *Littorina saxatilis* | 8 | 34.91 | 0.89 | 12.71 | 4.31 | 9.71 | 0.31 |
| Gastropoda | *Patella depressa* | 12 | 37.45 | 3.01 | 15.25 | 6.85 | 12.25 | 2.85 |
| Gastropoda | *Chaetopleura angulata* | 5 | 31.68 | 0.58 | 9.48 | 1.08 | 6.48 | −2.92 |
| Gastropoda | *Leptochiton algesirensis* | 6 | 32.33 | 2.04 | 10.13 | 1.73 | 7.13 | −2.27 |
| Gastropoda | *Patella vulgata* | 14 | 38.85 | 2.34 | 16.65 | 8.25 | 13.65 | 4.25 |
| Gastropoda | *Siphonaria pectinata* | 15 | 32.96 | 2.83 | 10.76 | 2.36 | 7.76 | −1.64 |
| Crustacea | *Pachygrapsus marmoratus* | 11 | 35.28 | 1.95 | 13.08 | 4.68 | 10.08 | 0.68 |
| Crustacea | *Carcinus maenas* | 6 | 36.00 | 0.00 | 13.80 | 5.40 | 10.80 | 1.40 |
| Crustacea | *Porcellana platyecheles* | 10 | 31.26 | 0.89 | 9.06 | 0.66 | 6.06 | −3.34 |
| Crustacea | *Pirimella denticulata* | 5 | 32.60 | 1.26 | 10.40 | 2.00 | 7.40 | −2.00 |
| Crustacea | *Anapagurus laevis* | 5 | 30.40 | 0.27 | 8.20 | −0.20 | 5.20 | −4.20 |
| Crustacea | *Necora puber* | 5 | 32.62 | 0.41 | 10.42 | 2.02 | 7.42 | −1.98 |
| Teleostei | *Atherina* sp. | 6 | 27.27 | 2.12 | 5.07 | −3.33 | 2.07 | −7.33 |
| Teleostei | *Diplodus cervinus* | 4 | 34.13 | 0.45 | 11.93 | 3.53 | 8.93 | −0.47 |
| Teleostei | *Liphophrys trigloides* | 3 | 32.97 | 0.75 | 10.77 | 2.37 | 7.77 | −1.63 |
| Echinodermata | *Marthasteria glacialis* | 7 | 33.01 | 1.70 | 10.81 | 2.41 | 7.81 | −1.59 |
| Echinodermata | *Asterina gibbosa* | 11 | 31.18 | 2.49 | 8.98 | 0.58 | 5.98 | −3.42 |
| Echinodermata | *Ophiura ophiura* | 7 | 29.77 | 1.31 | 7.57 | −0.83 | 4.57 | −4.83 |
| Cnidaria | *Actinia equina* | 3 | 35.67 | 1.76 | 13.47 | 5.07 | 10.47 | 1.07 |

certainly also have a crucial role in the outcome of warming effects on biota. However, if we don't have reference values of upper thermal limits of species in the beginning of the 21st century, by 2100 it will be hard or even impossible to distinguish an adapted species from a naturally thermally resistant species.

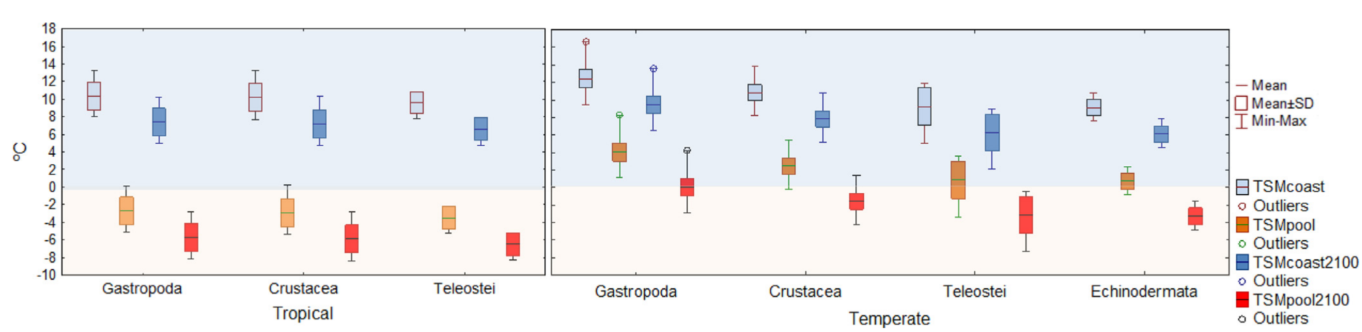


**Fig. 2.** Distribution of the values of Thermal Safety Margins (TSM) of tropical and temperate organisms, for coastal waters (TSMcoast), for tide pools (TSMpool), for coastal waters in the year 2100 (TSMcoast2100) and for tide pools in the year 2100 (TSMpool2100).

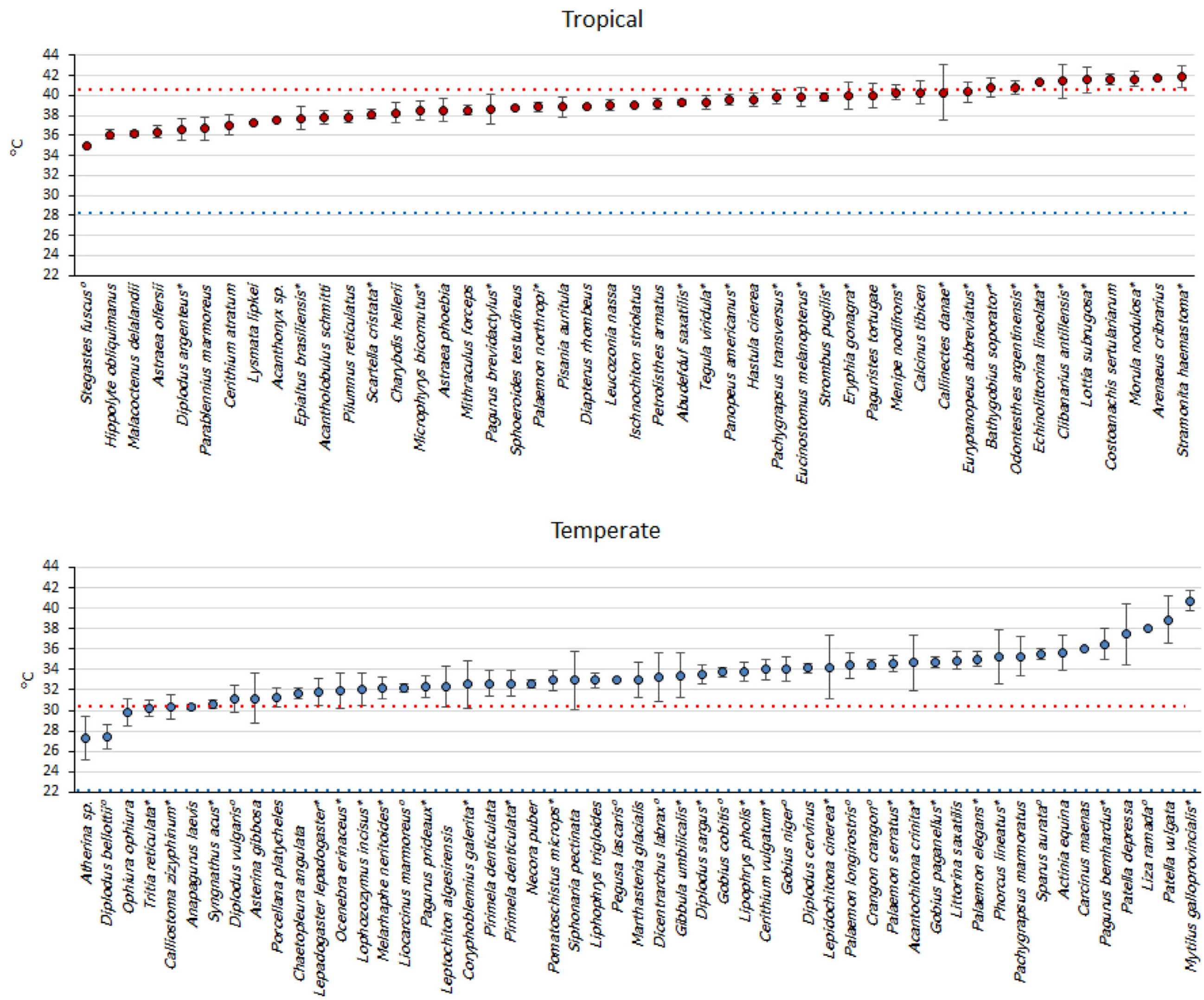


**Fig. 3.** CTMax values for 100 species tested in the field sites in the present and in past works (species tested in Vinagre et al 2016 are marked with a°, while those tested in Vinagre et al 2018 are marked with a*). Maximum habitat temperatures are indicated by the red line, for tide pools, and the blue line for coastal waters.

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